

1 Overlapping generations can balance the fluctuations in the activity  
2 patterns of an endangered ground beetle species: long-term monitoring of  
3 *Carabus hungaricus* in Hungary

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## 25 Abstract

- 26 1. *Carabus hungaricus* is a ground beetle inhabiting the Pannonian steppes. It is highly  
27 endangered by fragmentation and abandonment of its habitat.
- 28 2. For five consecutive years, from 2006 to 2010, we used the mark-release-recapture  
29 technique in a grid of 270 live-capture pitfall traps to study its population ecology in  
30 sandy grasslands on Szentendre Island in the Northern vicinity of Budapest, Hungary.
- 31 3. In total, 3950 individuals of *C. hungaricus* (1874 females and 2076 males) were marked.
- 32 4. Population size was estimated at ~2000 individuals per year; the estimates for females  
33 were consistently higher than for males. The minimum population size was  $1317 \pm 60.1$   
34 individuals in 2007, while the maximum was  $2169.7 \pm 108.8$  individuals in 2008.
- 35 5. Adults older than a year formed ~32-42% of the population, while individuals surviving  
36 for three years formed ~10%, and those surviving for four years formed ~2% of the  
37 population. Individuals older than four years comprised <1% of the population. Female  
38 survival rate was higher than that of male, but the capture rate also differed between  
39 sexes.
- 40 6. Although the studied population showed considerable fluctuations in the pattern of  
41 activity during the five years, its size seemed to be relatively stable, underlining the  
42 importance of overlapping generations.

43 Keywords: *Carabus hungaricus*; long-term monitoring; mark-recapture; sandy grasslands; time  
44 series; Natura 2000

## Introduction

The dry grasslands of Central Europe support distinct plant and animal assemblages (Medvedev, 1950; 1954; Medvedev & Shapiro, 1957; Petrusenko & Petrusenko, 1971; Eidelberg *et al.*, 1988; Penev, 1996; Putchkov, 2011; Cizek *et al.*, 2012), with many species endemic to the Pannonian biogeographical region (Varga, 1995). Thus, they are considered to be biodiversity hotspots (Cremene *et al.* 2005). Dry grasslands are vanishing rapidly; with less than five percent of the remaining steppe areas being in their natural state and only a fraction of them protected (Mader, 1983; Goriup 1998). Remaining grassland fragments are often too small to support viable populations of more specialized species; many grassland inhabitants are thus endangered and some have become locally extinct (Mader *et al.* 1990). In Hungary, the proportion of natural and semi-natural grassland areas has decreased from 2.7 to 0.7 million hectares since the 19th century (i.e. by 74%) (Hungarian Central Statistical Office, 2010). Most of the productive grasslands were converted to arable land; and the less productive parts such as sand steppes were turned to poplar (*Populus X euamericana* ), black pine (*Pinus nigra*), scots pine (*Pinus sylvestris*) and black locust (*Robinia pseudoacacia*) plantations after World War I (Anonymous, 1923). Infrastructural developments, such as road building and urbanization, increased during the course of the 20th century. These processes led to fragmentation of all habitat types and a further dramatic decline in the biodiversity of open habitats (Magura & Kődöböcz, 2007). Moreover, the intensification of agricultural practices, such as ploughing, soil tillage, and fertilizer usage, together with the spread of invasive plant species, such as common milkweed (*Asclepyas syriaca*), resulted in changes in plant species' composition and quality in most of the remaining dry grassland habitats in the Carpathian Basin (Török *et al.*, 2003).

Such habitat changes led also to decreases in the area, quality, and connectivity of dry grasslands, resulting in a dramatic decline of their biodiversity, including also arthropods (Rushton *et al.*, 1989; McLaughlin & Mineau, 1995; Magura & Kődöböcz, 2007). The magnitude of changes in

arthropod diversity can be estimated by the monitoring of groups sensitive to the above processes (Sieren & Firscher, 2002). Ground beetles (*Coleoptera*, *Carabide*) have been successfully used as indicators in many ecological studies (Mader, 1980; Lövei & Sunderland, 1996; McGeoch, 1998; Rainio & Niemelä, 2003; Samways, 2005). Despite that, little is known about the population biology/ecology of most species, including the large and attractive habitat specialists of the genus *Carabus* (e.g. Matern *et al.*, 2007). A number of studies deal with their reproduction, life cycle, and movement strategies (e.g. Rijnsdorp, 1980; Sota, 1987; Kobuta, 1996; Weber & Heimbach, 2001; Pokluda, 2012), while others have investigated the size of ground beetle populations (e.g. Greenslade, 1964; Nelemans *et al.*, 1989; Samu & Sárospataki, 1995; Thomas *et al.*, 1998; Holland & Smith, 1999; Griffiths *et al.*, 2005). Population size estimates of *Carabus* species are rare (Grüm, 1975; Hockmann *et al.*, 1992; Vainikainen *et al.*, 1998; Weber & Heimbach, 2001; Matern *et al.*, 2007). None of the papers mentioned above applied a detailed selection procedure to find a proper model for the estimations of population parameters. However, they do provide further details on their life histories and population structures and would be potentially useful for their conservation. In most of European countries, several *Carabus* species are red listed, legally protected, and often endangered (Niemelä, 2001). The European Union has listed several species of community importance - *Carabus hampei*, *C. hungaricus*, *C. menetriesi pacholei*, *C. olympiae*, *C. variolosus* and *C. zawadzskii* - in Annexes II and IV of the Habitat Directive (92/43/EEC: European Commission, 1992). *C. hungaricus* is considered to be a stenotopic tall-grass steppe-habitat specialist (Pokluda *et al.*, 2012), occurring mainly in dry calcareous and acidic sand grasslands in lowland areas, and dolomite grasslands on hills (Szél *et al.*, 2006; Bérces *et al.*, 2008). The distribution of *C. hungaricus* is highly fragmented even in Hungary, in its last stronghold (Bérces *et al.*, 2008). The beetle is endangered everywhere across its distribution range; it is almost extinct or critically endangered in several countries (Austria: Müller-Motzfeld, 2004; Czech Republic, Slovakia: Pokluda 2012; Moldova: Neculiseanu *et al.*, 1999; Turin *et al.*, 2003).

96 To allow for its effective conservation, an extensive monitoring program of *C. hungaricus* was  
97 initiated by the Duna-Ipoly National Park, Hungary. Here we present the main results of a five-  
98 year study dealing with the temporal changes of major population parameters and analyze the key  
99 factors affecting survival of this highly endangered, tall-grass sand steppe specialist, including: (i)  
100 seasonal activity patterns; (ii) estimation of the major population parameters, such as population  
101 size, between-year survival, and capture probability; (iii) identification of the trends in the capture  
102 data by the decomposition of the time series and its components; and (iv) prediction of future  
103 trends based on the identified temporal patterns in capture data.

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105

## 106 Material and methods

### 107 *Study area and sampling design*

108 The study was carried out on the Szentendrei Island, a 30 km long, 0.5-3.5 km wide island  
109 surrounded by the Danube River, located about 30 kilometers North of Budapest, Hungary. Natural  
110 floodplain forests and poplar plantations dominate the shores of the island, while arable lands,  
111 human settlements (three villages) and forest plantations such as black locust, black pine and scots  
112 pine cover large areas in the core of the island. There are two larger, and one smaller sand dune  
113 areas on the island, all belonging to the authority of the Duna-Ipoly National Park, and it is a Site of  
114 Community Importance with the appellation of “HUDI20047 Szigeti homokok”. One such area  
115 near the village of Pócsmegyer (about 170ha, 100-120 m a.s.l.) comprising 40 ha (see appendix-  
116 1.kml) is covered with tall-grass vegetation of the Pannonian sand steppes (*Festucetum vaginatae*)  
117 and was selected as the study site. These grasslands are fragmented by patches of black locust  
118 plantations (*Robinia pseudoacacia*). Pannonian sand steppe vegetation is characterized by the  
119 dominant bunch grasses *Stipa borystenica*, *Chrysopogon gryllus* and *Festuca vaginata*. No  
120 management took place at the sampling area during the study period, while the surrounding areas

121 were irregularly mown. Mean annual precipitation is between 550-600 mm, and the mean annual  
122 temperature is 10°C (min.: -14°C and max.: +34°C) (Dövényi *et al.*, 2010).

123 Two hundred and seventy live-capture, non-baited pitfall traps were placed in a 4×4m grid in 10  
124 rows and 27 columns, covering an area of 0.4 ha (see appendix-1.kml). Each trap contained 2 cups,  
125 the larger ones (9 cm diameter, with a volume of 0.5 l) were dug into the ground. The smaller cups  
126 (with a diameter of 9 cm and volume of 0.3 l) were inserted into the larger ones in order to empty  
127 the traps more easily. Cups were perforated at the bottom and covered by a plastic roof to avoid  
128 penetration of water. The traps were checked weekly from March to December each year between  
129 2006 and 2010; the sampling thus covered the whole activity period of *C. hungaricus* (Bércecs *et al.*,  
130 2008).

131

#### 132 *Marking the individuals*

133 Beetles were individually marked by numbers, engraved on their elytra with a small drill. After  
134 marking, beetles were released, approximately 1.5 m NE of the trap. On release, beetles usually  
135 hide among grass/litter on the spot. Handling and marking caused no obvious mortality nor harm to  
136 the beetles. The sex and visible injuries or anomalies of each individual were recorded in a  
137 database.

138

#### 139 *Data analysis - Estimating the demographic parameters of the studied population*

140 Demographic parameters of the *C. hungaricus* population were estimated using constrained linear  
141 modeling (CLM), which applies the framework of generalized linear modeling (glm: Lebreton *et*  
142 *al.*, 1992). This approach provides high flexibility in the estimation of parameters and the  
143 opportunity to compare the models based on information theoretic approaches (i.e. AIC, AICc).

144 The *C. hungaricus* population was considered as an open population, due to fact that capture  
145 occasions (i.e. years) were distant in time and mortality and births occurred between them

146 (Baillargeon & Rivest, 2007). Cormack-Jolly-Seber and Jolly-Seber models have been fitted for the  
147 open populations (Cormack, 1985; 1989) followed by a loglinear approach to estimate survival ( $\Phi$ )  
148 and the number of new units entering into the population ( $B$ ) between the studied years. Capture  
149 rate ( $p$ ) and population size ( $N$ ) were estimated for each year of the study. Total number of  
150 individuals inhabiting the survey area ( $N_{total}$ ) was also estimated for each year. Two types of  
151 Poisson regression models using the glm approach were fitted in order to consider properly the  
152 temporal effects in the mark-recapture data; 1) an open model with unconstrained capture  
153 probabilities (varying between years), and 2) an open model with equal capture probabilities  
154 (common value for capture probabilities between years). In the first case it was not possible to  
155 estimate the requested parameters for the first and last capture occasions (i.e. years). Models were  
156 fitted on the whole population (full data matrix), and separately for females and males. The mark-  
157 recapture survey followed a robust design, thus the data matrix was converted to primary session  
158 data (i.e. years) with the consideration of the secondary sampling sessions (i.e. number of sampling  
159 occasions within a year). Models were compared based on their deviance, degrees of freedom and  
160 AIC values. The goodness of the model fit was tested by the deviance of the standard model based  
161 on the Pearson residuals against the number of captures. Large residuals indicated bad fit of the  
162 data. Thus they were removed and the models were re-fitted, compared and tested again.

### 163 *Estimating trends in time*

164 The identification of overall trends in long-term datasets requires techniques that are able to  
165 distinguish between seasonal differences and global trends. In our studies we followed the protocol  
166 suggested by Zucchini & Nemadić (2011). The decomposition of time series was applied through a  
167 non-parametric regression technique for the capture data between 2006-2010. This method  
168 performed a seasonal decomposition of a given time series ( $X_t$ ) by determining the trends ( $T_t$ ) using  
169 local polynomial regression and calculating the seasonal component ( $S_t$ ) (and residuals) from the  
170 differences  $X_t - T_t$  (Cleveland *et al.*, 1990; Zucchini & Nemadić 2011). To predict the possible

171 number of captures in the population for the following year, ARIMA [autoregressive integrated  
 172 moving average, which is the generalisation of autoregressive moving average (ARMA) models]  
 173 time series models were fitted to the capture data (or Box Jenkins approach, Brockwell & Davis,  
 174 1996; Ripley, 2002). This modeling process takes advantage of associations in the sequentially  
 175 lagged relationships that usually exist in periodically collected data. The formula of the ARIMA  
 176 model is:

$$177 \quad \Delta I Z_t = \Phi_1 Z_{t-1} + \dots + \Phi_p Z_{t-p} + a_t - \theta_1 a_{t-1} - \dots - \theta_q a_{t-q}$$

178 where:

179  $\Delta I Z_t$  – differenced time series (i.e.  $Z_t - Z_{t-1}$ )

180  $Z_t$  – set of the possible observations on the time-sequenced random variable,

181  $a_t$  – random shock term at time  $t$

182  $\Phi_1 \dots \Phi_p$  – autoregressive parameter of order  $p$

183  $\theta_1 \dots \theta_q$  – moving average parameter for order  $q$ .

184 Sample autocorrelation and partial autocorrelation functions were used to identify the ARIMA  
 185 model in the appropriate order. The model's estimates were obtained using a maximum likelihood  
 186 method and diagnostics included the Akaike Information Criterion and the residual analysis by  
 187 Ljung-Box. Since the residuals of a well-fitted model are distributed randomly (Box & Pierce,  
 188 1970; Ljung & Box, 1978) the statistics examined the null of the independently distributed  
 189 residuals. Thus, the final model was the result of several iterations of identifications, estimations  
 190 and diagnostic processes based on the conventional criteria for the model's adequacy. All analyses  
 191 were carried out in R 2.13.1 (R Development Core Team, 2011) using the package Rcapture for  
 192 capture-recapture analysis (Baillargeon & Rivest, 2007).

193



194

## 195 Results

196 *Major activity patterns*197 During the five years we marked 3950 *C. hungaricus* individuals (1874 females and 2076 males).

198 Twenty five - thirty three percent of individuals were recaptured in the year after marking, and

199 &lt;10% of individuals were recaptured later (i.e. in the second, third or fourth year after the year of

200 marking); the main decline in the recaptures appeared after the second year (Table 1).

201 The activity pattern showed distinct periodicity (Fig. 1) characterized by two activity peaks within a

202 year. During the first activity peak (from mid-May and mid-July), females were more active than

203 males. The second peak was characterized by high activity of males from early August to October.

204 Larvae were caught from the end of October to the early May.

205

206 *Estimation of population parameters*

207 For females, models with unconstrained capture probabilities provided better fit (smaller deviation)

208 and lower estimates than models with equal capture probabilities (Table 2). The two model types

209 provided similar estimates for males. In order to compare the differences among years, we

210 considered the results of models with equal capture probabilities, which provided estimates for all

211 the years studied. Estimated survival rates varied between 32-42%, and were the highest in 2007

212 and 2008, with significant between-year variation. Survival rates for females were usually higher

213 than that of males (except in 2007-2008, see Table 3). The number of newly-marked individuals

214 varied between ~600-1000 per year, the highest being between 2007-2008 (Table 3). The number of

215 new entrants per sex showed variation between periods, also showing the highest estimates in 2007-

216 2008. The capture probabilities of males were higher than those of females, especially in 2007

217 (Table 4, Fig. 2A). The estimated population size ranged from 1317 ( $\pm 60.1$ ) to 2169.7 ( $\pm 108.8$ )

218 individuals per year, with the number of females being consistently higher than that of males (Table

219 4). The population size decreased between 2006 and 2007, reaching the highest abundance during  
220 the study period in 2008 and decreasing thereafter monotonously towards 2010 (Fig. 2B).

221

### 222 *Trends and seasonality*

223 A clear and distinct seasonal pattern has been found in the capture data based on the decomposition  
224 of time series. A bimodal pattern was found with an earlier and a later activity peaks (Fig. 3). A  
225 between-year pattern showed a slight increase in the number of captures in 2006 and a strong  
226 decrease in 2007. The second high activity period was characterized by an activity peak in 2008,  
227 with a slight decline in 2009. In 2010, this overall pattern (high activity in every other year) was  
228 intended to return (Fig. 3). We found that the optimum ARIMA model was the most useful, with  
229 (2,2,5) for the captures (log likelihood = -517.82, AIC = 1051.63). The residuals indicated small  
230 variation around the mean zero; none of them was greater than the double standard deviations, thus  
231 this model fitted best. The autocorrelation of the residuals was not significantly different from zero  
232 as a set, and had a constant variance, thus confirming the adequacy of the model (Box-Pierce test,  
233  $X^2 = 0.017$ ,  $df = 1$ ,  $p = 0.89$ ). The observed mean (with S.E.) of captures was  $78.93 \pm 12.82$ . Based on  
234 the models the expected mean value of the captures for the following three years were  $79.11 \pm 59.18$ .  
235 The portrayed number of captures with the predictions indicated a slight decrease in the number of  
236 captures in the subsequent three years (Fig. 4).

237

238

### 239 Discussion

240 No data on the population ecology of *C. hungaricus* have been published prior to this study. Our  
241 long-term “mark-recapture” study proved that an abundant population inhabited the sandy  
242 grasslands of the Szentendrei Island. Although there was considerable variation in activity during

243 the five-year study, the population size of *C. hungaricus* seemed relatively stable. The high  
244 proportion of beetles surviving for more than one year seemed to reduce fluctuations in population  
245 size between the years, and might be the key for persistence of isolated populations of this species.

#### 246 *Activity patterns*

247 The seasonal activity has been divided into two main activity regimes in the studied  
248 population. Matern *et al.* (2007) found similar bimodal activity pattern for a typical spring breeder,  
249 *Carabus variolosus*. The activity pattern of *C. hungaricus* can be explained by its phenology, which  
250 starts with adults emerging in June causing the first peak of activity. After a short aestivation in July  
251 and the first half of August, the high male activity detected corresponded to the breeding season,  
252 similarly to other species (eg. Brunsting, 1981; Kegel, 1990; Kennedy, 1994; Drees & Huk, 2000).  
253 The activity of the adults had almost ceased by the end of reproduction. Larvae appeared at the end  
254 of October and they were active during the winter period. Second and third instar larvae developed  
255 in spring (March-May); low (peculiar) activity of overwintering adults could be observed during  
256 this time (Szél *et al.*, 2006; Bérces *et al.*, 2007).

257 One of the most important results of our study was that a large proportion of the individuals  
258 (32-42% estimated) contribute to reproduction in the following year. Although this phenomenon  
259 had already been described for other carabids (Schjötz-Christiansen, 1965; den Boer, 1971;  
260 Thiele, 1977; Sharova *et al.*, 2005), its magnitude was unknown. Based on the above-mentioned  
261 facts, we suppose that many *C. hungaricus* individuals are able to spread the risk of encountering  
262 unsuitable conditions (e.g. dry or cold) over several years, thus reducing fluctuations in population  
263 size and the chance of sudden extinction due to stochastic and other reasons (den Boer, 1971).

#### 264 *Estimated population parameters and size*

265 A relationship between the activity and capture probability, corresponding to the fact that  
266 higher activity leads to higher captures (e.g. Thomas *et al.*, 1998; Konvicka *et al.*, 2005; Matern *et*  
267 *al.*, 2007) was detected in the studied population of *C. hungaricus*. Females had lower capture rates

268 than males, while their survival rate was higher. This suggests that higher male activity during the  
269 mating season might lead to an increased mortality, due to e.g. predation. A similar observation was  
270 made for *Pterostichus melanarius* where males' daily dispersal distance was considerable higher  
271 than that of females, resulting in more males caught (Thomas *et al.*, 1998).

272 The estimation of the population size showed that a stable population of ~2000 individuals  
273 inhabited the studied sandy grassland in Hungary. The highest difference in population size  
274 between years was ~850 individuals. The observed fluctuations in the size of the population  
275 studied over the five years were thus rather low. Especially considering that insect populations  
276 typically exhibit strong fluctuations (Samways, 2005), and the fluctuation of carabid populations  
277 can change by a factor of five (Grüm, 1986), and even ten, as observed for *C. arvensis* during a  
278 nine-year study (Turin *et al.*, 2003). Lower fluctuations are more likely to appear in the  
279 populations of forest-dwelling *Carabus* species (Weber & Heimbach 2001; Günther & Assman  
280 2004; Matern *et al.*, 2007). For example for an isolated *C. variolosus* population consisting of  
281 ~200 individuals, Matern *et al.* (2007) suggested that the population was large enough to maintain  
282 a viable population with evolutionary potential, based on the 50/500 rule by Franklin (1980). The  
283 studied population thus exhibited rather low fluctuations and seems viable in the long term.

284

#### 285 *Decomposition of time series and predictions*

286 The decomposition of the time series data proved that there was a considerable trend in the  
287 five-year capture data suggesting a high activity regime every other year. There are only a few  
288 studies published on the long-term monitoring of ground beetles (Sieren & Fisher 2002; Scott &  
289 Anderson, 2003; Desender *et al.*, 2007), but these concern the assemblage level, the use of different  
290 techniques and approaches. Although Scott & Anderson (2003) suggest that six- or seven-year data  
291 should be sufficient to find trends in datasets, their paper was based on data from 19 sites in the UK,  
292 and the spatial differences could be the responsible factor for the lack of clear trends in their data.

293 Hunter & Price (1998) found that time series analysis was a powerful tool for understanding insect  
294 population dynamics, especially for *Hymenoptera*. This could also help in forecasting agricultural  
295 pest densities in arable lands (Szentkirályi, 2002). Matern *et al.*, (2007) suggest that the long-term  
296 monitoring of the endangered *C. variolosus* may contribute to identifying the fluctuation in the  
297 population dynamics and the critical points of its phenology.

298

## 299 Conclusions

300 The long-term monitoring of *C. hungaricus* suggests that the size of the studied population was  
301 relatively stable, and seemed large enough to ensure long-term survival. Overlapping generations  
302 contribute to the stability of the studied population. Due to fragmentation and habitat size, the  
303 population remains susceptible to management, and monitoring should continue. This is also  
304 consistent with the fact that Hungary is in the “high biodiversity responsibility class” due to the  
305 high ratio of unique habitat types and endemic species, especially of invertebrates (Schmeller *et al.*,  
306 2008) in Europe.

307

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316

## 317 References

- 318 Anonymous (1923) 1923. évi XIX. törvénycikk az alföldi erdő telepítéséről és a fásításokról  
319 Kihirdettetett az Országos Törvénytar 1923. április 25. napján kiadott 6. számában. [The XIX.  
320 Law of the year 1923 about the Hungarian Great Plain afforestation]
- 321 Baillargeon, S. & Rivest, L-P. (2007) Rcapture: loglinear models for capture-recapture in R.  
322 *Journal of Statistical Software*, **19**, <<http://www.jstatsoft.org/v19/i05>> 14th November 2011
- 323 Bérces, S., Szél, Gy., Ködöböcz, V., Kutasi, Cs., Szabó, K., Fülöp, D., Péntes, Zs. & Peregovits, L.  
324 (2007) A magyar futrinka (*Carabus hungaricus*). *A Kárpát-medence állatvilágának kialakulása*  
325 (ed. by L. Forró), pp. 107–124, Magyar Természettudományi Múzeum, Budapest
- 326 Bérces, S., Szél, Gy., Ködöböcz, V., & Kutasi, Cs. (2008) The distribution, habitat types and nature  
327 conservation value of a Natura 2000 beetle, *Carabus hungaricus* Fabricius, 1792 in Hungary  
328 *Back to the roots or back to the future? Towards a new synthesis between taxonomic, ecological*  
329 *and biogeographical approaches in carabidology. Proceedings of the XIII European*  
330 *Carabidologists Meeting, Blagoevgrad*, (ed. by L. Penev; T. Erwin and T. Assmann) pp 363-372,  
331 Pensoft Inc., Sofia, Bulgaria
- 332 Boer, P.J. den (1971) Stabilisation of animal numbers and the heterogeneity of the environment: the  
333 problem of the persistence of sparse populations. *Dynamics of populations: proceedings of the*  
334 *advanced study institute on dynamics of numbers in populations* (ed. by P.J. Den Boer and G.R.  
335 Gradwell), pp. 77-79, Center for Agricultural Publishing and Documentation, Oosterbeek,  
336 Netherlands.
- 337 Box, G.E.P. & Pierce, D.A. (1970) Distribution of residual correlations in autoregressive-integrated  
338 moving average time series models. *Journal of the American Statistical Association*, **65**, 1509-  
339 1526.
- 340 Brockwell, P.J. & Davis, R.A. (1996) *Introduction to time series and forecasting*. Springer, New  
341 York, USA.
- 342 Brunsting, A.M.H. (1981). Distribution patterns, life cycle and phenology of *Pterostichus*  
343 *oblongopunctatus* F. (Col., Carabidae) and *Philonthus decorus* Grav. (Col., Staphylinidae).

- 344 *Netherlands Journal of Zoology*. 31, 418–452.
- 345 Cizek, L., Hauck, D. & Pokluda, P. (2012) Contrasting needs of grassland dwellers: habitat  
346 preferences of endangered steppe beetles (Coleoptera). *Journal of Insect Conservation*, **16**, 281–  
347 293.
- 348 Cleveland, R.B., Cleveland, W.S., McRae, J.E., & Terpenning, I. (1990) STL: A seasonal-trend  
349 decomposition procedure based on loess. *Journal of Official Statistics* **6**, 3-73.
- 350 Cormack, R.M. (1985) Example of the use of GLIM to analyze capture-recapture studies. *Lecture*  
351 *notes in statistics 29: statistics in ornithology* (ed. by B.J.T. Morgan and P.M. North) pp 242–  
352 274, Springer-Verlag, New York, USA.
- 353 Cormack, R.M. (1989) Loglinear models for capture-recapture. *Biometrics*, **45**, 395–413.
- 354 Cremene, C., Groza, G., Rakosy, L., Schileyko, A.A., Baur, A., Erhardt, A. & Baur, B. (2005)  
355 Alterations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspots.  
356 *Conservation Biology* **19**, 1606–1618.
- 357 Desender, K., Maelfait, J.P. & Baert, L. (2007) Ground beetles as “early warning-indicators” in  
358 restored salt marshes and dune slacks. *Restoration of Coastal Ecosystems* (ed. by M. Isermann,  
359 and K. Kiehl).pp 25–39. Coastline reports, The Coastal Union Leiden, The Netherlands.
- 360 Drees, C. & Huk, T. (2000) Sexual differences in locomotory activity of the ground beetle *Carabus*  
361 *granulatus* L. *Natural history and applied ecology of Carabid beetles* (ed. P. Brandmayr), pp  
362 131-136, Pensoft, Sofia, Bulgaria.
- 363 Dövényi Z., Ambrózy P., Juhász Á., Marosi S., Mezősi G., Michalkó G., Somogyi S., Szalai Z. &  
364 Tiner T. (2010). *Magyarország kistájainak katasztere (Inventory of microregions in Hungary)*. pp  
365 25-29, HAS Geographical Research Institute, Budapest, Hungary.
- 366 Eidelberg, M.M., Maltzev, I.V., & Pervakov, V.P. (1988) The species composition of ground beetles  
367 (Coleoptera, Carabidae) of the Crimea. *Ekologia i taksonomiya nasekomykh Ukrainy*. pp. 61–68,  
368 Naukova Dumka, Kiev, Ukraine [in Russian].
- 369 European Commission (1992) *Council Directive 92/43/EEC of 21 May 1992 on the conservation of*  
30

370 *natural habitats and of wild fauna and flora,*

371 [http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index\\_en.htm](http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm) 11th

372 November 2011.

373 Franklin, I.R. (1980) Evolutionary change in small populations. *Conservation Biology, An*

374 *Evolutionary–Ecological Perspective* (ed. by M.E. Soulé and B.A. Wilcox). pp 135-150,

375 Sinauer, Sunderland, M.A., USA.

376 Goriup, P. (1998) The Pan-European biological and landscape diversity strategy: integration of

377 ecological agriculture and grassland conservation. The lowland grasslands of Central and

378 Eastern Europe. *Parks* **8**, 37-46.

379 Greenslade, P.J.M. (1964) The distribution, dispersal and size of a population of *Nebria brevicollis*

380 (F.), with comparative studies on three other Carabidae. *The Journal of Animal Ecology* **33**, 311-

381 333.

382 Griffiths, G.J.K., Alexander, C.J., Birt, A., Holland, J.M., Kennedy, P.J., Perry, J.N., Preston, R. &

383 Winder, L. (2005) A method for rapidly mass laser-marking individually coded ground beetles

384 (Coleoptera: Carabidae) in the field. *Ecological Entomology* **30**, 391-396.

385 Grüm, L. (1975) An attempt to estimate production of a few *Carabus* L. species (Col., Carabidae),

386 *Ekologia Polska* **23**, 673–680.

387 Grüm, L. (1986) Density fluctuations in a carabid guild. *Carabid beetles. Their adaptations and*

388 *dynamics*. (ed. by P.J. den Boer, M.L. Luff, D. Mossakowski & Weber) pp 344-359, Fischer,

389 Stuttgart, Germany.

390 Günther, J. & Assman, T. (2004) Fluctuations of carabid populations inhabiting an ancient

391 woodland (Coleoptera, Carabidae) *Pedobiologia* **48**, 159-164.

392 Hockmann, P., Menke, K., Schlomberg, P. & Weber, F. (1992) Untersuchungen zum individuellen

393 Verhalten (Orientierung und Aktivität) des Laufkäfers *Carabus nemoralis* im natürlichen

394 Habitat. *Abhandlungen aus dem Landesmuseum für Naturkunde zu Münster in Westfalen* **54**, 65-

395 98.



- 396 Holland, J.M. & Smith, S., (1999) Sampling epigeal arthropods: an evaluation of fenced pitfall traps  
397 using mark-release-recapture and comparisons to unfenced pitfall traps in arable crops  
398 *Entomologia Experimentalis et Applicata* **91**, 347-357.
- 399 Hungarian Central Statistical Office (2010) *Hungarian online databases*, <<http://www.ksh.hu>> 12th  
400 November 2010.
- 401 Hunter, M.D. & Price, P.W. (1998) Cycles in insect populations: delayed density dependence or  
402 exogenous driving variables? *Ecological Entomology* **23**, 216-222.
- 403 Kegel, B. (1990) Diurnal activity of Carabid beetles living on arable land. *The role of ground*  
404 *beetles in ecological and environmental studies*. (ed. by N.E. Stork), pp 65-76, Intercept,  
405 Newcastle, UK.
- 406 Kennedy, P.J. (1994) The distribution and movement of ground beetles in relation to set-aside arable  
407 land. *Carabid Beetles: Ecology and Evolution* (ed. by K. Desender, M. Dufrêne, M. Loreau, M.  
408 L. Luff, and J.P. Maelfait), pp 439-444, Kluwer Academic, Dordrecht, The Netherlands.
- 409 Kobuta, K. (1996) Movements of three *Carabus (Ohomopterus)* species and a hybrid population  
410 (Coleoptera, Carabidae). *Japanese Journal of Entomology* **64**, 861-869.
- 411 Konvicka, M., Čížek, O., Filipová, L., Fric, Z., Beneš, J., Křupka, M., Zámečník, J. & Dočkalová,  
412 Z. (2005) For whom the bells toll: Demography of the last population of the butterfly  
413 *Euphydryas maturna* in the Czech Republic. *Biologia*, **60**, 551-557.
- 414 Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modelling survival and testing  
415 biological hypotheses using marked animals: a unified approach with case studies. *Ecological*  
416 *Monographs* **62**, 67-118.
- 417 Ljung, G.M. & Box, G.E.P. (1978) On a measure of lack of fit in time series models. *Biometrika* **65**,  
418 297-303.
- 419 Lövei G.L. & Sunderland KD (1996) Ecology and behaviour of ground beetles (Coleoptera:  
420 Carabidae). *Annual Review of Entomology* **41**, 231-256.
- 421 Mader, H.J. (1980) Die Verinselung der Landschaft aus tierökologischer Sicht. *Natur und*

422 *Landschaft* **55**, 91-96.

423 Mader, H.J. (1983) Warum haben kleine Inselbiotope hohe Artenzahlen? *Natur und Landschaft* **10**,  
424 367-370.

425 Mader, H.J., Schell, C. & Kornacker, P. (1990) Linear barriers to arthropod movement in the  
426 landscape. *Biological Conservation* **54**, 209-222.

427 Magura T. & Ködöböcz V. (2007) Carabid assemblages in fragmented sandy grasslands.  
428 *Agriculture, Ecosystems & Environment* **119**, 396-400.

429 Matern, A., Drees, C., Meyer, H. & Assmann, T. (2007) Population ecology of the rare carabid  
430 beetle *Carabus variolosus* (Coleoptera: Carabidae) in north-west Germany. *Journal of Insect*  
431 *Conservation* **12**, 591-601.

432 McGeoch, M.A. (1998) The selection, testing and application of terrestrial insects as bioindicators.  
433 *Biological Reviews* **73**, 181-201.

434 McLaughlin, A. & Mineau, P. (1995) The impact of agricultural practices on biodiversity.  
435 *Agriculture, Ecosystems & Environment* **55**, 201-212.

436 Medvedev, S.I. (1950) Coleoptera. *Zhivotnyi mir SSSR. T. 3. Zona steppei*. pp 294–347, Moskva-  
437 Leningrad, Russia [in Russian]

438 Medvedev, S.I. (1954) Peculiarities in the distribution of some ecological forms of insects in  
439 various landscape zones of Ukraine. *Zool zhurnal*, **33**, 1245–1262. [in Russian]

440 Medvedev, S.I. & Shapiro, D.C. (1957) A contribution to the knowledge of beetles (Coleoptera) of  
441 the Moldavian SSR and adjacent areas of Ukraine. *Uchenie zapiski Kharkovskogo universiteta*  
442 **30**, 173–206. [in Russian]

443 Müller-Motzfeld, G. (2004) Band 2. Adephaga 1: Carabidae (Laufkäfer). *Die Käfer Mitteleuropas*  
444 (ed. by H. Freude, K.W. Harde, G.A. Lohse, & B. Klausnitzer). Spektrum-Verlag, Heidelberg-  
445 Berlin, Germany.

446 Neculiseanu, Z., Danila, A. & Cilipic, G. (1999) Lista insectelor rare si amenintate cu disparitia din  
447 Republica Moldova.

- 448 <[http://www.salvaeco.org/insecte/page/carabus\\_pachistus\\_hungaricus.php](http://www.salvaeco.org/insecte/page/carabus_pachistus_hungaricus.php)> 27th November  
449 2005.
- 450 Nelemans, M.N.E., den Boer, P.J. & Spee, A. (1989) Recruitment and summer diapause in the  
451 dynamics of a population of *Nebria brevicollis* (Coleoptera: Carabidae). *Oikos* **56**, 157-169.
- 452 Niemelä, J. (2001) *Carabid beetles (Carabidae) and habitat fragmentation: a review. European*  
453 *Journal of Entomology* **98**, 127-132.
- 454 Penev, L. (1996) Large-scale variation in carabid assemblages, with special reference to the local  
455 fauna concept. *Annales Zoologici Fennici* **33**, 46-63.
- 456 Petrusenko, A. & Petrusenko, S.V. (1971) A study of ground beetle fauna of meadows and steppe of  
457 the Ukraine. *Zbirnik pratz Zool. musea AS of Ukraine. Kyiv*, **34**, 60–64. [in Ukrainian]
- 458 Pokluda, P., Hauck, D. & Cizek, L. (2012) Importance of marginal habitats for grassland diversity:  
459 fallows and overgrown tall-grass steppe as key habitats of endangered ground-beetle *Carabus*  
460 *hungaricus*. *Insect Conservation and Diversity* **5**: 27-36.
- 461 Putschkov, A. (2011) Ground beetles of the Ukraine (Coleoptera, Carabidae) *ZooKeys* **100**, 503–515.
- 462 R Development Core Team (2011) R: *A language and environment for statistical computing. R*  
463 *Foundation for Statistical Computing*, Vienna, Austria. ISBN 3-900051-07-0, <[http://www.R-](http://www.R-project.org/)  
464 [project.org/](http://www.R-project.org/)> 24th November 2011.
- 465 Rainio, J. & Niemelä, J. (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators.  
466 *Biodiversity & Conservation* **12**, 487-506.
- 467 Rijnsdorp, A.D. (1980) Patterns of movement in and dispersal from a Dutch forest of *Carabus*  
468 *problematicus* (Coleoptera, Carabidae). *Oecologia* **45**, 274–281.
- 469 Ripley, B.D. (2002) Time series in R 1.5.0. *R News* **2**, 2-7. <[http://www.r-](http://www.r-project.org/doc/Rnews/Rnews_2002-1.pdf)  
470 [project.org/doc/Rnews/Rnews\\_2002-1.pdf](http://www.r-project.org/doc/Rnews/Rnews_2002-1.pdf)> 13th October 2011.
- 471 Rushton, S.P., Luff, M.V. & Eyre, M.D. (1989) Effect of pasture improvement and management on  
472 the ground beetle and spider communities of upland grasslands. *Journal of Applied Entomology*  
473 **26**, 489-503.

- 474 Samways, M.J. (2005) *Insect Diversity Conservation*. Cambridge University Press, Cambridge, UK.
- 475 Samu F. & Sárospataki M. (1995) Estimation of population sizes and home ranges of polyphagous  
476 predators in alfalfa using mark-recapture: an exploratory study (*Cicindela campestris*, *Pardosa*  
477 *agrestis*). *Arthropod natural enemies in arable land I. Density, spatial heterogeneity and*  
478 *dispersal*. (ed. by S. Toft and W. Riedel) *Acta Jutlandica* **70**, 47-55.
- 479 Scott, W. & Anderson, R. (2003) Temporal and spatial variation in carabid assemblages from the  
480 United Kingdom Environmental Change Network. *Biological Conservation* **110**, 197-210.
- 481 Schjötz-Christiansen B. (1965) Biology and population studies of Carabidae of the  
482 Corynephoretum. *Natura Jutlandica* **11**, 1-173.
- 483 Sharova, I.K. & Khobrakova, L.T. (2005) Features of the life cycles of *Pterostichus montanus*  
484 (Motschulsky, 1844) and *Carabus loschnikovi* (Fischer-Waldheim, 1822) (Coleoptera,  
485 Carabidae) in conditions of the mountain taiga belt in the Eastern Sayan. *Seriya Biologicheskaya*  
486 **32**, 27-37.
- 487 Schmeller, S.D., Gruber, B., Bauch, B., Lanno, K., Budrys, E., Badij, V., Juskaitis, R., Sammul, M.,  
488 Varga, Z. & Henle, K. (2008) Determination of national responsibilities for species conservation  
489 in regions with multiple political jurisdictions. *Biodiversity & Conservation* **17**, 3607-3622.
- 490 Sieren, E. & Firscher, F.P. (2002) Evaluation of measures for enlargement, renaturation and  
491 development of a dry grassland biotope by analysing differences in the carabid fauna  
492 (Coleoptera). *Acta Oecologica* **23**, 1-12.
- 493 Sota, T. (1987) Mortality *pattern* and age *structure* in two carabid populations with different  
494 *seasonal life cycles*. *Researches on Population Ecology* **29**, 237-254.
- 495 Szentkirályi, F. (2002) Fifty-year-long insect survey in Hungary: T. jermy's contributions to light-  
496 trapping. *Acta Zoologica Academiae Scientiarum Hungaricae* **48**, 85-105.
- 497 Szél, Gy., Bérces, S., Kutasi, Cs. & Ködöböcz, V. (2006) A magyar futrinka (*Carabus hungaricus*  
498 Fabricius, 1792) hazai elterjedése és élőhelyei. *Praenorica Folia Historico- Naturalia* **9**, 45-80.
- 499 [Distribution and habitats of *Carabus hungaricus* Fabricius, 1792 in Hungary (Coleoptera:

500 Carabidae.]] in Hungarian.

501 Thiele HU (1977) *Carabid beetles in their environments: A study on habitat selection by*  
502 *adaptations in physiology and behaviour*. Springer-Verlag, Berlin, Germany.

503 Thomas, C.F.G., Parkinson, L. & Marshall, E.J.P. (1998) Isolating the components of activity-  
504 density for the carabid beetle *Pterostichus melanarius* in farmland. *Oecologia* **116**, 103-112.

505 Török, K., Botta-Dukát, Z., Dancza, I., Németh, I., Kiss, J., Mihály, B. & Magyar, D. (2003)  
506 Invasion Gateways and Corridors in the Carpathian Basin: Biological Invasions in Hungary.  
507 *Biological Invasions* **5**, 349–356.

508 Turin, H., Penev, L. & Casale, A. (2003) *The Genus Carabus L. in Europe. A synthesis. Fauna*  
509 *Europaea Evertebrata No 2*. Pensoft, Sofia, Bulgaria

510 Vainikainen, V., Itaemies, J., Pulliainen, E. & Tunkkari, P. (1998) Mobility, population size and life  
511 time pattern of *Carabus glabratus* (Coleoptera, Carabidae) under extreme northern forest  
512 conditions. *Entomologica Fennica* **9**, 217-224.

513 Varga, Z. (1995) Geographical Patterns of Biodiversity in the Palearctic and in the Carpathian  
514 Basin. *Acta Zoologica Academiae Scientiarum Hungaricae* **41**, 71-92.

515 Weber, F. & Heimbach, U. (2001) Behavioural, reproductive and developmental seasonality in  
516 *Carabus auronitens* and *Carabus nemoralis* (Col., Carabidae). A demographic comparison  
517 between two co-existing spring breeding populations and tests for intra- and interspecific  
518 competition and for synchronizing weather events. *Mitteilungen aus der Biologischen*  
519 *Bundesanstalt für Land- und Forstwirtschaft Berlin-Dahlem* **382**, 1-192.

520 Zucchini, W. & Nemadić, O. (2011) *Time series analysis in with R part I*.

521 <<http://www.statock.wiso.uni->

522 [goettingen.de/veranstaltungen/zeitreihen/sommer03/ts\\_r\\_intro.pdf](http://www.statock.wiso.uni-goettingen.de/veranstaltungen/zeitreihen/sommer03/ts_r_intro.pdf)> 13th October 2011

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524

525 Table 1. The number of *Carabus hungaricus* individuals marked on Szentendrei Island, Hungary  
 526 between 2006-2010, and their recaptures over those years. The first line shows the number of  
 527 individuals newly marked each year. Below, the number (and percentage) of beetles recaptured  
 528 after a given period.

529

	<i>2006</i>	<i>2007</i>	<i>2008</i>	<i>2009</i>	<i>2010</i>
no. of newly captured adults	1008 (100)	559 (100)	1053 (100)	743 (100)	587 (100)
	2006-2007	2007-2008	2008-2009	2009-2010	
Alive after 2 y	256 (25.4)	185 (33.1)	276 (26.2)	188 (25.3)	
	<i>2006-2008</i>	<i>2007-2009</i>	<i>2008-2010</i>		
Alive after 3 y	104 (10.3)	50 (8.9)	13 (2.3)		
	<i>2006-2009</i>	<i>2007-2010</i>			
Alive after 4 y	21 (2.1)	13 (2.3)			
	<i>2006-2010</i>				
Alive after 5 y	4 (0.4)				

530

531 Table 2. Model diagnostics and total population (*N*<sub>total</sub>) size of *Carabus hungaricus* on Szentendrei  
532 Island, Hungary between 2006 and 2010.

<i>Models</i>	<i>Deviance</i>	<i>df</i>	<i>AIC</i>	<i>N</i> <sub>total</sub> ± <i>S.E.</i>
<i>Overall</i>				
unconstrained “ <i>p</i> ” model	22.16	15	155.47	4881.54 ± 139.26
equal “ <i>p</i> ” model	31.62	19	171.28	5968.47 ± 208.77
<i>Females</i>				
unconstrained “ <i>p</i> ” model	15.96	17	143.14	2734.19 ± 132.11
equal “ <i>p</i> ” model	26.07	21	158.7	3143.62 ± 157.86
<i>Males</i>				
unconstrained “ <i>p</i> ” model	26.27	17	149.7	2682.71 ± 93.96
equal “ <i>p</i> ” model	29.30	19	149.67	2954.071 ± 121.86

533

534 Table 3. Estimated survival( $\Phi$ ) and number of births ( $B$ ), with standard error for *C. hungaricus* on  
 535 Szentendre Island, Hungary between 2006-2010. The column “Est.” denotes the estimated  
 536 parameters by the models.

<i>Models</i>	<i>Est.</i>	<i>2006-2007</i>	<i>2007-2008</i>	<i>2008-2009</i>	<i>2009-2010</i>
overall unconstrained “ <i>p</i> ” model	$\Phi$	0.33±0.04	0.41±0.04	0.29±0.03	NA
	$B$	NA	1301.8±135.7	1028.4±125.2	NA
overall equal “ <i>p</i> ” model	$\Phi$	0.35±0.02	0.42±0.03	0.32±0.02	0.39±0.02
	$B$	680.8±50.9	1614.8±98.3	1072.8±54.8	826.4±46
female unconstrained “ <i>p</i> ” model	$\Phi$	0.44±0.05	0.34±0.04	0.41±0.05	NA
	$B$	NA	666.5±95.4	737.9±125.4	NA
female equal “ <i>p</i> ” model	$\Phi$	0.4±0.03	0.41±0.03	0.37±0.03	0.42±0.04
	$B$	388.7±39.2	849.6±66.3	532.2±45.2	420.1±39
male unconstrained “ <i>p</i> ” model	$\Phi$	0.35±0.03	0.42±0.05	0.36±0.04	NA
	$B$	NA	733.3±78.5	858.1±116.9	NA
male equal “ <i>p</i> ” model	$\Phi$	0.33±0.02	0.44±0.04	0.31±0.02	0.40±0.03
	$B$	308.6±31.6	815.6±61	543.5±35.1	410±29

537

538



539 Table 4. Estimated capture probabilities ( $p$ ) and overall population size ( $N$ ) with standard error for  
 540 *C. hungaricus* on Szentendrei Island, Hungary between 2006 and 2010. The column “Est” denotes  
 541 the estimated parameters by the models.

<i>Models</i>	<i>Est.</i>	<i>2006</i>	<i>2007</i>	<i>2008</i>	<i>2009</i>	<i>2010</i>
overall unconstrained “ $p$ ” model	$p$	NA	0.48±0.05	0.68±0.05	0.68±0.08	NA
	$N$	NA	1541.4±126.5	1942±131.9	1596.4±176.1	NA
overall equal “ $p$ ” model	$p$	0.59±0.03	0.59±0.03	0.59±0.03	0.59±0.03	0.59±0.03
	$N$	1773.8±95.6	1317±60.1	2169.7±108.8	1787.7±94	1533.5±89.6
female unconstrained “ $p$ ” model	$p$	NA	0.41±0.05	0.59±0.07	0.40±0.05	NA
	$N$	NA	902.4±116.2	977.6±110.8	1144.3±153.6	NA
female equal “ $p$ ” model	$p$	0.49±0.03	0.49±0.03	0.49±0.03	0.49±0.03	0.49±0.03
	$N$	953±73.8	769.9±56.1	1172.5±84.5	973.3±69.9	831.3±65.2
male unconstrained “ $p$ ” model	$p$	NA	0.59±0.05	0.69±0.06	0.43±0.05	NA
	$N$	NA	669±53.4	1015.6±86.9	1226±124.4	NA
male equal “ $p$ ” model	$p$	0.65±0.04	0.65±0.04	0.65±0.04	0.65±0.04	0.65±0.04
	$N$	876.4±55.9	604.2±32.8	1083.6±65.3	882±54.9	765.7±53.1

542

543

544 Figure legends:

545 Fig 1. One-year activity pattern of *C. hungaricus* based the captures from 2008. The lines indicate  
546 the trends in the captures based on the simple moving average for three neighbouring points.  
547 Sampling occasions' dates: S1, S2-first and second sampling occasion respectively, the two-  
548 digit number after the occasion denotes the month as a number (e.g. 03 = March). Legend: line  
549 with full circle – captures for males; line with empty circle-captures for females; solid line-  
550 trend for males; dashed line – trend for females.

551 Fig 2. Estimated capture rate (A) and population size (B) for *C. hungaricus*  
552 on Szentendre Island, Hungary between 2006 and 2010. These estimations based on the equal  $p$   
553 model per sexes.

554 Fig 3. Seasonal decomposition of time series data for *C. hungaricus* on Szentendre Island, Hungary  
555 between 2006 and 2010. The data denote the original structure of time series data, the seasonal  
556 indicates the within-year variation patterns, while the trend denotes the global (between-year)  
557 patterns in the dataset. The remainder shows unexplained variances.

558 Fig 4. Observed capture data (solid black line) along the forecast by ARIMA models (dashed line  
559 denotes standard errors of the predicted values) for the next three years for *C. hungaricus*.

560

561